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THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA

IV. THE DICYNODONT FAUNA

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The dicynodonts described in this paper were collected by the 1964-1965 expedition of the Museo de la Plata and the Museum of Comparative Zoology to the Permo-Triassic of western Argentina (Romer, 1966). Nearly all come from the Chañares Formation, the lithology and stratigraphic relationships of which have been described by Romer and Jensen (1966). They state (p. 12) that, "With one exception, all of the numerous vertebrate fossils found in the Chañares were from the lowest 10 meters or so of the formation." Eighteen dicynodont specimens were found in this fossiliferous band. One of these belongs to a new genus and species of dicynodont, described here as *Chanaria platiceps*. Eight specimens belong to a new species closely allied to *Dinodontosaurus turpior* from the Santa Maria Formation of Brazil (Cox, 1965); it is here named *Dinodontosaurus brevirostris*. Another specimen belongs to a second new species of this genus, here named *D. platygynathus*. Finally, an isolated large scapulocoracoid and clavicle show the presence of another genus of dicynodont. The remaining seven specimens are incomplete or badly damaged and therefore cannot be assigned with certainty to any of the named taxa.

In the accompanying figures, oblique shading indicates broken bone surface, horizontal shading indicates the presence of matrix, and broken lines indicate restored outlines of bone. The following abbreviations are used: MCZ — the Museum of Comparative Zoology, Harvard University; BYU — the Earth Sciences Museum, Brigham Young University, Provo, Utah; DGM — Divisão de Geologia e Mineralogia, Ministerio das Minas e Energia, Rio de Janeiro.

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CHANARIA gen. nov.

Type species: *C. platyceps* sp. nov.

Diagnosis. Dicynodont of moderate size: skull length 33 cm. Teeth absent except for upper tusks. Greatest width of skull is across occipital region. Blunt anterior end to snout. Tusk projects anteroventrally. Lacrimal extends forwards on face, probably meets septomaxilla. No bony bosses on snout or on pineal region. Interorbital bar fairly wide. Frontal extends anteriorly into nasal as rectangular midline projection. Quite large prefrontal. Preparietal present, forming anterior border of pineal foramen. Postorbital bone extends well behind pineal foramen. Intertemporal bar narrow but concave in cross-section, not ridged. Squamosal does not extend on to intertemporal bar, posterior end of which is formed by interparietal. Short, wide temporal opening. Low, wide occiput; supraoccipital does not extend high up in midline.

CHANARIA PLATYCEPS sp. nov.

Holotype. No. 65-XI-14-3 Museo de la Plata, La Plata, Argentina, skull. Collected by the 1964-1965 expedition of the Museo de la Plata and the Museum of Comparative Zoology.

Horizon and locality. From an exposure in the Triassic Chañares Formation about 6 miles east of the point where the Chañares River emerges into the Campo de Talampaya, in western La Rioja Province, Argentina.

Description. The type skull is 33 cm long and 30 cm wide. The mid-region of the palate, both quadrate regions, and part of the left side of the skull are missing.

Dorsal view (Fig. 1). The premaxilla extends a considerable distance posteriorly in the midline. There is only a short midline nasal suture, for the posterior regions of the nasals are separated by a rectangular anterior projection of the frontals. There is quite a large prefrontal; the posterior end of its suture with the frontal is uncertain, owing to damage. The interorbital bar is of moderate breadth.

The postorbital bone extends back to a point halfway between the pineal foramen and the posterior end of the intertemporal bar. The intertemporal bar is quite narrow, but it is slightly concave from side to side, without any midline ridge. The extreme posterior end of the bar is formed by the interparietal.

The occipital wing of the squamosal extends laterally, not posterolaterally. As a result, the posterior edge of the skull is almost straight and runs transversely, and the temporal opening is almost quadrilateral, its width approximately equalling its length.

Occipital view (Fig. 2). The occiput is rather low, its midline region being little higher than its more lateral parts. Most of the midline surface above the foramen magnum is formed by the interparietal rather than by the supraoccipital. The bones of the central occipital plate are fused together. The quadrate region and outer edge of the lateral wing of the squamosal are missing, but the dotted outline shown is the minimum extent of squamosal necessary to accommodate a quadrate of normal size.

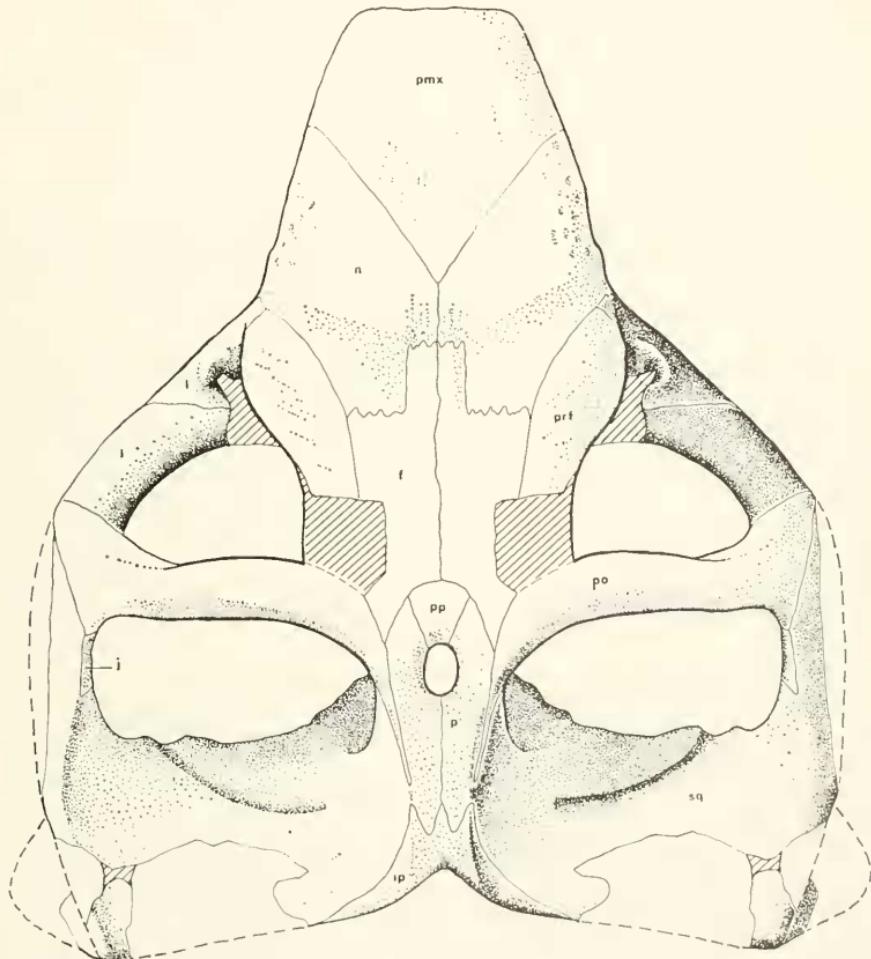


Figure 1. *Chanaria platyceps*, type specimen. Dorsal view of skull, $\times \frac{1}{3}$ (for abbreviations, see p. 26).

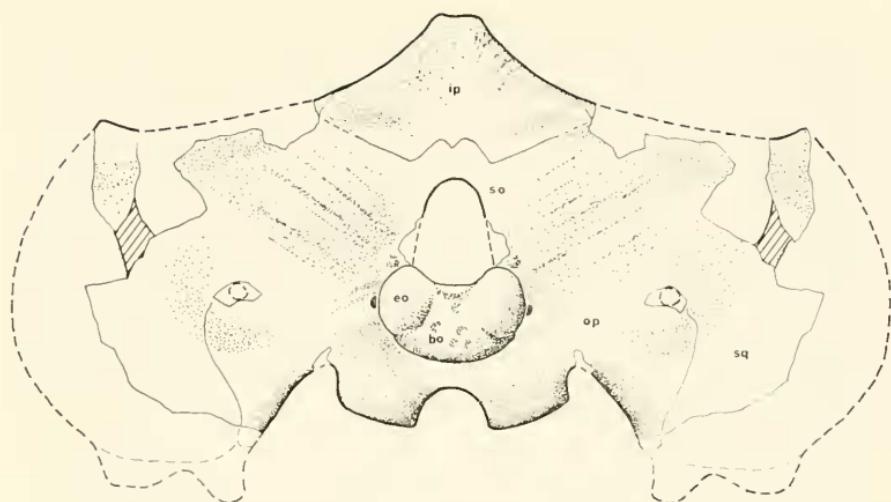


Figure 2. *Chanaria platyceps*, type specimen. Occipital view of skull. $\times \frac{1}{3}$ (for abbreviations, see p. 26).

Lateral view (Fig. 3). The powerful tusks project anteroventrally. The squamosal runs forward to meet the maxilla under the front half of the orbit.

A groove runs anteroventrally from the anterior corner of the nostril to the edge of the snout. A ridge which forms the lower edge of this groove also extends posteriorly along the maxilla behind the nostril. Above this ridge both the maxilla and the lacrimal curve slightly inwards, so that there is no sharply defined posterior border to the nostril. The lacrimal extends a considerable distance anteriorly and, though its anterior end and most of the septomaxilla are missing, it seems very probable that these two bones met, separating the nasal from the maxilla.

The palatal surface of the premaxilla bears the pair of anterior ridges and the median posterior ridge that are normal in the dicynodonts. The remainder of the ventral region of the skull is too incomplete to show any features of value.

Taxonomic position. In an earlier paper (Cox, 1965) I suggested that two main families of Triassic dicynodonts could be distinguished on the basis of the shape of the snout, the presence or absence of a median crest along the intertemporal bar, and the proportions of the occiput and of the temporal opening. In *Chanaria* the snout is wide and blunt, there is no median crest along

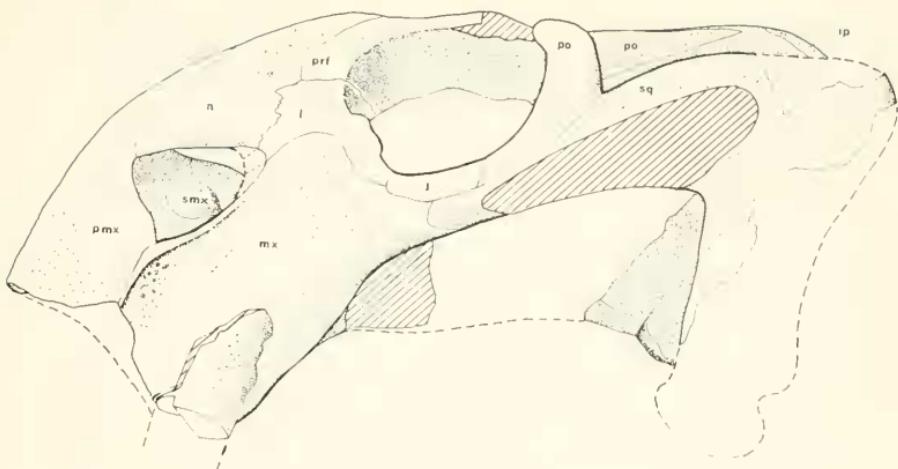


Figure 3. *Chanaria platyceps*, type specimen. Lateral view of skull, $\times \frac{1}{3}$ (for abbreviations, see p. 26).

the intertemporal bar, the occiput is wide but low, and the temporal opening is short. In all these characteristics, *Chanaria* clearly belongs to the family Stahleckeriidae.

Bonaparte (1966a) has since disagreed with my proposed classification of the Triassic dicynodonts into separate families. He believes that these forms are very uniform in structure, and that they are monophyletic in origin. Though I do not agree with either of these beliefs, Bonaparte's views and my own are, in the absence of knowledge of the Permian ancestry of the Triassic forms, subjective views of equal validity. The truth will emerge only from further work on the dicynodonts of the late Permian and early Triassic, and further discussion on these alternative classifications may be postponed until relevant material has been found and studied.

DINODONTOSAURUS BREVIROSTRIS sp. nov.

Holotype. No. 65-XI-14-4 Museo de la Plata, La Plata, Argentina, skull. Collected by the 1964-1965 expedition of the Museo de la Plata and the Museum of Comparative Zoology.

Horizon and locality. From an exposure in the Triassic Chañares Formation about 6 miles east of the point where the Chañares River emerges into the Campo de Talampaya, in western La Rioja Province, Argentina.

Referred specimens. Specimen Nos. 3452-3457, Museum of Comparative Zoology, Harvard; specimen No. MR-120, Earth Sciences Museum, Brigham Young University, Provo, Utah.

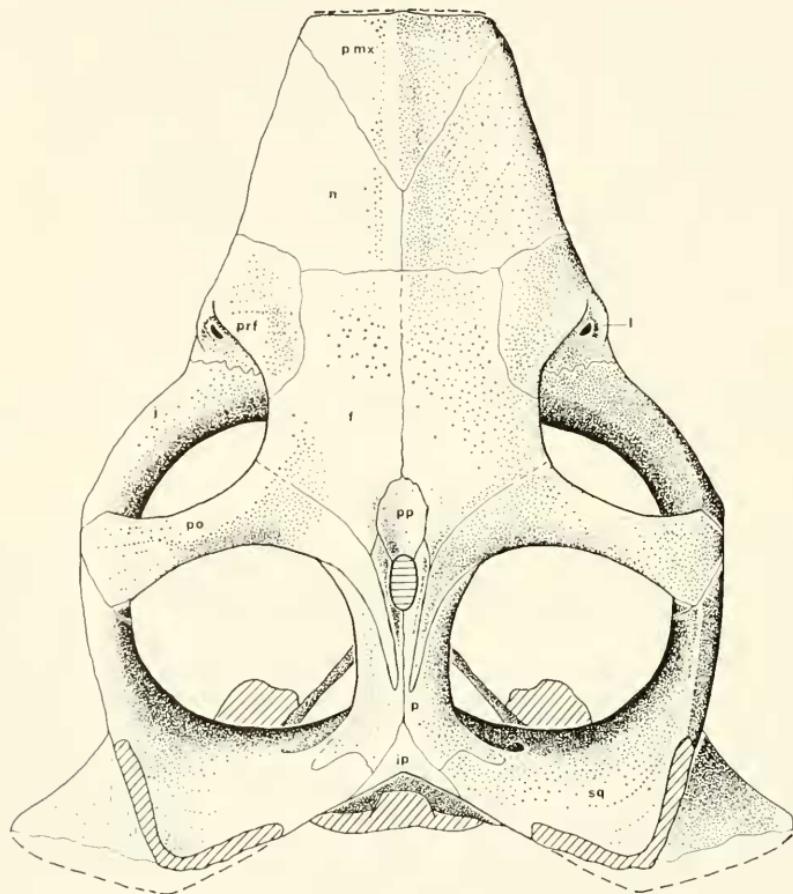


Figure 4. *Dinodontosaurus brevirostris*, type specimen. Dorsal view of skull, $\times \frac{1}{3}$ (for abbreviations, see p. 26).

Description. The skull of the type specimen, and those of specimens MCZ Nos. 3453 and 3457 and of specimen BYU No. MR-120, are all about 30 cm long. Specimen MCZ No. 3454 is 23 cm long and appears to be a juvenile. Other dicynodont remains from the Chañares Formation which cannot be certainly identified but which probably belong to this, the commonest dicynodont in the fauna, show that specimens nearly twice as large as the type were present.

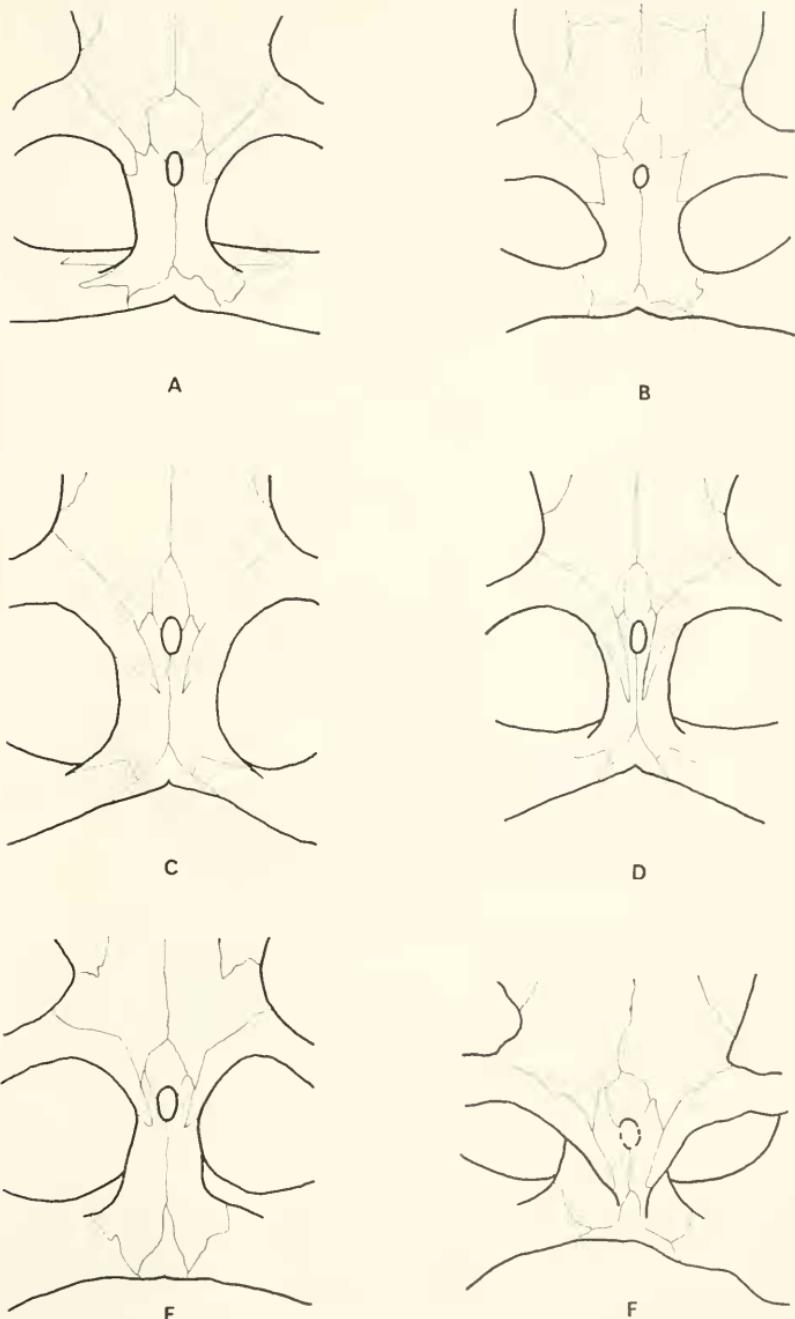


Figure 5. Dorsal views of pineal areas of specimens of *Dinodontosaurus*, reduced to equal size. A, D. *turpior*, MCZ No. 1628; B, D. *turpior*, MCZ No. 1687; C, D. *brevirostris*, MCZ No. 3454; D, D. *brevirostris*, type specimen; E, D. *turpior*, DGM No. 530R; F, D. *turpior*, DGM No. 213R.

Dorsal view (Fig. 4). *D. brevirostris* has the short temporal region and narrow, ridged intertemporal bar which are characteristic of the genus. However, there are some differences between *D. brevirostris* and the type species, *D. turpior*, in the relationships of the postorbital to the pineal opening. The postorbital of *D. brevirostris* approaches quite closely to the side of the pineal opening, and also extends posteriorly well beyond it. Though there is considerable range of variation in these characteristics in *D. turpior* (Fig. 5), the postorbital in that species is not normally as extensive as that of *D. brevirostris*.

Ventral view. The palate of the type specimen of *D. brevirostris* is too poorly preserved to show anything of value, but this area is well shown in the smaller specimen, MCZ No. 3454 (Fig. 6). The secondary palate extends posteriorly to a point level with the root of the canine tusks. The vomer and palatines do not form a bony

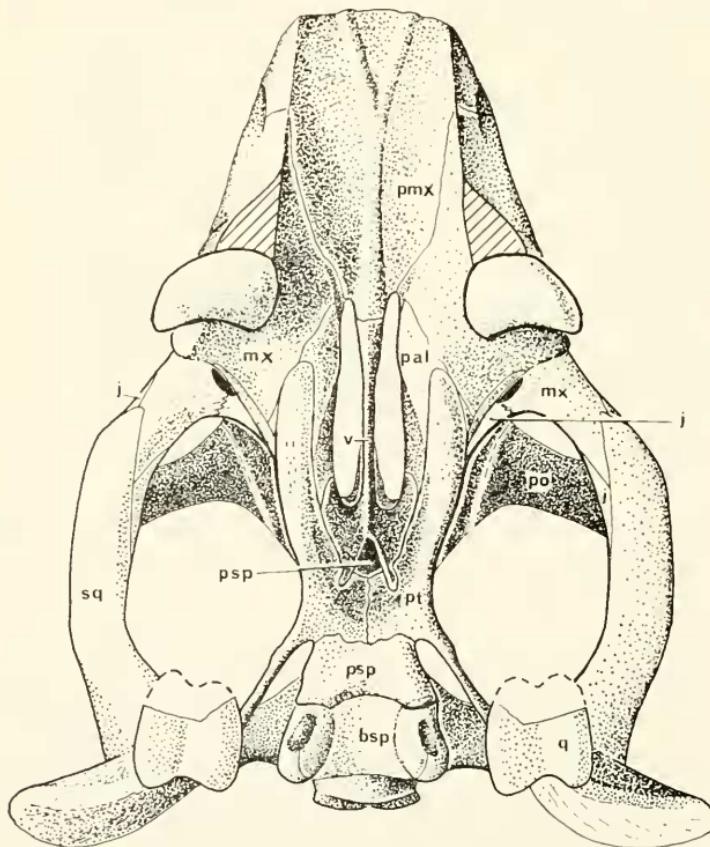


Figure 6. *Dinodontosaurus brevirostris*, MCZ No. 3454. Ventral view, x 4/9 (for abbreviations, see p. 26).

roof to the anterior part of the primary palate, between the anterior rami of the pterygoids. On either side of the median blade of the vomer there is therefore a clear passage dorsally (in the bony skull) to the ventral side of the bones of the skull roof (see also Fig. 9B). Behind the vomer, only a relic of the interpterygoid vacuity remains; through it is visible the ventral surface of the processus cultriformis of the parasphenoid.

The only specimen of *D. turpior* in which the median region of the palate is well preserved is specimen DGM No. 530R. In this¹ the vomer and palatines form a bony roof over a greater extent of the posterior part of the primary palate, and the median fusion of the pterygoids has extended further forward within the interpterygoid vacuity, so that the processus cultriformis is not visible from

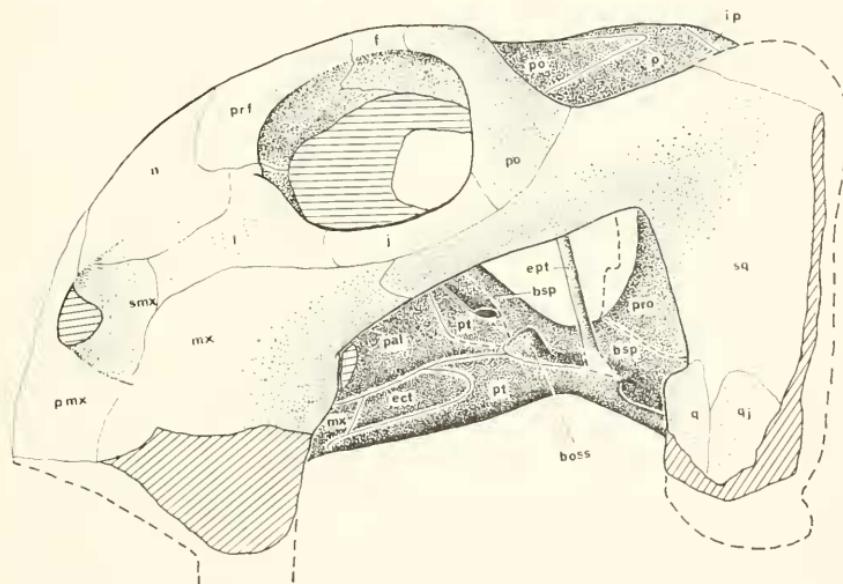


Figure 7. *Dinodontosaurus brevirostris*, type specimen. Lateral view, $\times \frac{1}{3}$ (for abbreviations, see p. 26).

¹This specimen is of particular interest because it was described in 1936 by Tupí Caldas under the name *Diodontosaurus pedroanum*, a name which predates Romer's description of *Dinodontosaurus* (1943). However, Tupí Caldas's description is unfortunately so brief and so poorly illustrated that it cannot be regarded as a satisfactory basis for the identification of a new taxon, and *Diodontosaurus pedroanum* must therefore be regarded as a *nomen nudum*. The specimen has recently been more fully figured by Beltrão (1966).

below. However, it would be unjustifiable to assume that the two species differ in these features, as the smaller extent of these bones in specimen MCZ No. 3454 could merely be a result of its relative immaturity.

Side view (Fig. 7). The external naris is rather damaged but appears to be shallow, and there are no large foramina in the region of the septomaxilla. Though the edge of the maxilla where it forms the margin of the mouth is somewhat damaged, it is thin and was probably sharp-edged. This edge descends ventroposteriorly so that it reaches a considerable distance down the anterior border of the tusk.

Comparison of *D. brevirostris* with the specimens of *D. turpior* in the Museum of Comparative Zoology suggested that the snout of the Argentinian species was very much shorter, and the tusk much more ventrally directed, than in the Brazilian species. However, I was fortunately able to visit Rio de Janeiro and study the excellent material of *D. turpior* in the Divisão de Geologia e Mineralogia, Ministerio das Minas e Energia. This material has been prepared under the direction of Mr. L. I. Price, who has also made extensive studies of it. Examination of this material soon showed that the skull of specimen MCZ No. 1670 is very unusual in its long, low shape, and that there is a considerable range of variation in this region in *D. turpior* (Fig. 8). Nevertheless, there do appear to be two constant differences between the snouts of the two species. Firstly, the external naris of *D. brevirostris* is much closer to the anterior edge of the premaxilla than is that of *D. turpior*. Secondly, the tusk of *D. brevirostris* always projects directly ventrally, so that there is an abrupt angle between the body of the maxilla and the anterior end of the zygomatic arch, whereas there is a smoother transition between these regions in *D. turpior*. It is worth noting also that the lacrimal extends further forward on the face and meets the septomaxilla in all specimens of *D. brevirostris* in which the sutures of these regions are visible. This condition is known in *D. turpior* (Fig. 8F), but in that species these two bones are often separated by the maxilla.

There is a prominent boss on the dorsal surface of the palate, anterior to the base of the epipterygoid. This boss lies above a very distinct curving suture which separates it from the pterygoid, and it is therefore formed by the basisphenoid. Restudy of this area in *D. turpior* shows an identical situation, despite my statement that the boss in that species "is clearly part of the pterygoid" (Cox, 1965:482). Camp and Welles (1956:fig. 49) also show this boss as part of the basisphenoid in *Daptocephalus leoniceps*.

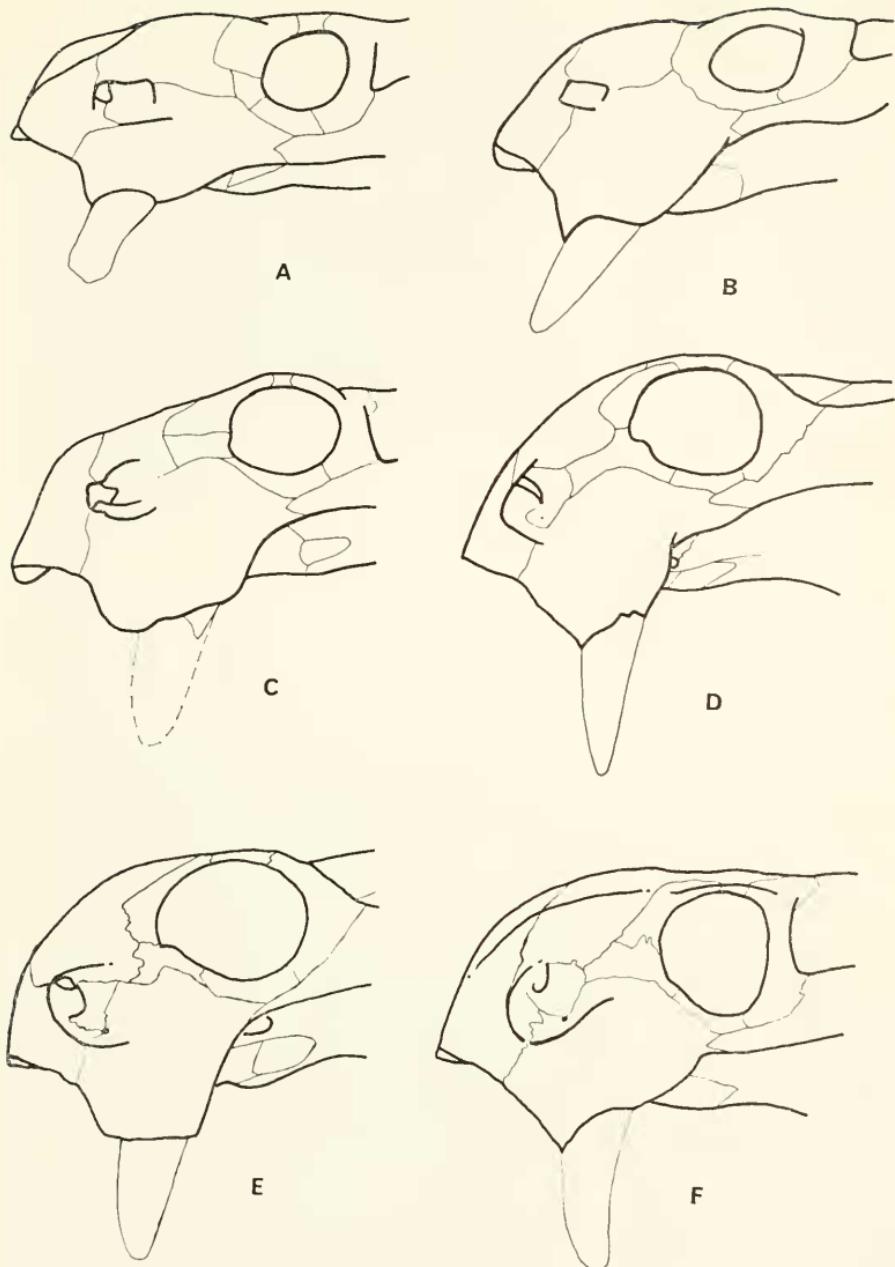


Figure 8. Lateral views of snouts of specimens of *Dinodontosaurus*, reduced to equal size. A, *D. turpior*, MCZ No. 1670; B, *D. turpior*, MCZ No. 1687; C, *D. turpior*, MCZ No. 1628; D, *D. brevirostris*, MCZ No. 3454; E, *D. turpior*, DGM No. 530R; F, *D. turpior*, DGM No. 309.

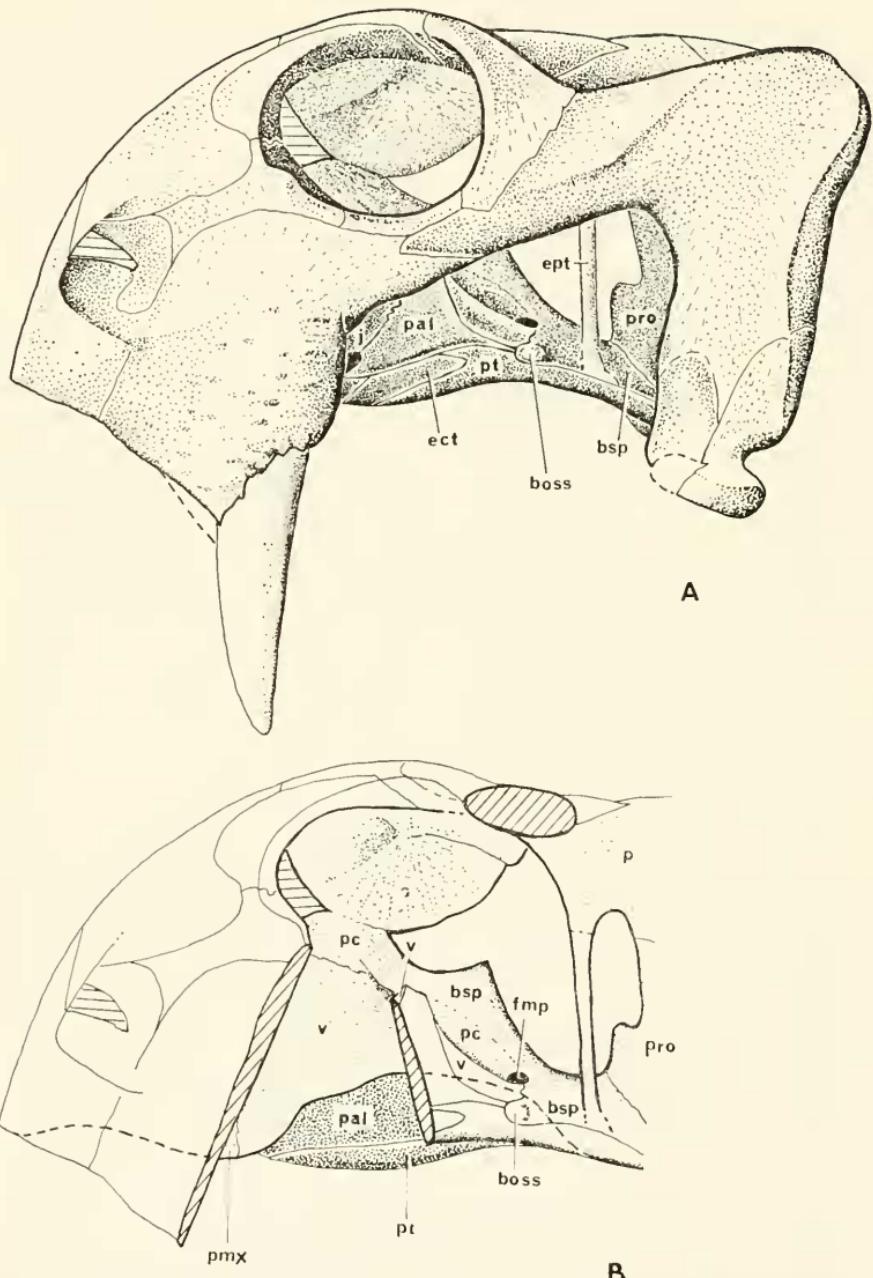


Figure 9. *Dinodontosaurus brevirostris*, MCZ No. 3454. Lateral views, $\times 4/9$, A, of complete skull; B, after removal of suborbital bar, postorbital bar, anterior end of left half of palate, and part of left maxilla. Dotted lines in figure B show ventral outlines of midline regions of premaxilla, vomer and pterygoid (for abbreviations, see p. 26).

Further information on the structure of the dorsal roof of the palate and of the median interorbital-internasal septum is provided by specimen MCZ No. 3454 (Fig. 9A, B). This shows clearly that the ectopterygoid is present, confirming my earlier tentative identification of this bone in *D. turpior* (Cox, 1965). The palatine has an extensive exposure on the dorsal surface of the palate. It forms the lower border of the large foramen which runs forwards into the dental cavity of the maxilla; it extends dorsally to contact the parasphenoid, and runs back to meet the basisphenoid. Much of the palatine overlies the lateral wing of the vomer, which is visible in front of the palatine and also above its posterior extension, where the vomer forms the lower border of the dorsal end of the canal which runs forwards and upwards from the interpterygoid vacuity. As Klaauw and Roon (1942) have pointed out, this opening is not the simple equivalent of the old interpterygoid vacuity, and they have suggested that it be called the fenestra medio-palatalis. The canal was probably traversed by a blood vessel. Since no such blood vessel is known in either *Sphenodon* (O'Donoghue, 1920) or *Ctenosaura* (Oelrich, 1956), it is impossible to identify it, though it seems most likely to have been a branch of the palatine artery.

Above the fenestra medio-palatalis lies the medial region of the parasphenoid-basisphenoid complex. The processus cultriformis of the parasphenoid, as is normal in synapsids, continues anteriorly beyond the basisphenoid, and receives the lower edge of the sphenethmoid. The processus cultriformis is underlain by the vomer. This medial part of the vomer forms the lower part of the interorbital septum and also the posterior part of the internasal septum. It extends ventrally to meet the posterior end of the median palatal ridge of the premaxilla and has a total depth of 5.5 cm. The more dorsal portion of the interorbital septum is formed by the sphenethmoid (Fig. 9B).

More posteriorly, much of the rod-like epipterygoid is preserved in the young specimen, but its lower edge is damaged and the position of its suture with the parietal dorsally is uncertain. There are clear sutures between the prootic and the parietal, and between the prootic and the parasphenoid-basisphenoid complex.

All the specimens of *D. brevirostris* are tusked. Most of the tusks are broken off short, but the whole of the right tusk of specimen MCZ No. 3453 is preserved and shows clear signs of wear. The outer surface of the distal end of the tusk is worn, so that its tip lies near its posteromedial edge. Traces of other wear facets

are also visible on the posteromedial surface of this specimen, but are better shown in an isolated tusk, specimen MCZ No. 3452 (Fig. 10A-C).

In longitudinal section of a tusk, the dentine appears to consist of a series of V-shaped bands; in a tusk about 15 cm long and 2.5 cm in diameter at its base, these bands are about 2.5 mm thick (Fig. 10E). They are caused by alternating light and dark zones of dentine, which are apparently due to slight variations in the concentration or thickness of the dental tubules. Further bands, which are similar but only a few tenths of a millimetre in diameter, are also visible in thin sections examined under a microscope.

A system of cracks, which in general parallel this system of V-shaped bands in the dentine, can also be seen in longitudinal section (Fig. 10D), and appear as concentric circles in transverse section of the tusk. A similar system has been described in *Placerias* and *Kannemeyeria* by Camp and Welles (1956). However, these cracks are not related to the above-mentioned variations in the structure of the dentine, and appear to be post-mortem. The cracks merely reflect the main plane of structural weakness in the dentine, which in turn is related to its mode of deposition.

The base of the tusk is open and it probably grew continuously. A series of annular grooves can also be seen around that portion of the tusk which lies within the maxilla; this has also been noted by Camp and Welles (1956). Similar annular grooves and variations in dental structure (alternating between columnar and marbled dentine) have been described in the elephant seal *Mirounga leonina* by Laws (1953). He has shown that the pattern of banding in that animal is complex, but that there is a regular annual repetition of this pattern. The details of the annual pattern also differ between the sexes, due to their different cycles of activity during the breeding season. It is unfortunately impossible to verify whether these features in *Dinodontosaurus* are similarly related to age or sex. This would be expected only if the climate were sufficiently seasonal to cause variations in the rate of growth of both sexes, or if variations resulted from such seasonal activities as egg-laying.

Postcranial material. Specimens MCZ Nos. 3454, 3455 and 3456 all included postcranial material; that belonging to specimen MCZ No. 3455 is particularly well preserved. However, none of this material shows significant differences from the corresponding bones of *D. turpior*, or adds to our knowledge of the postcranial skeleton of the genus.

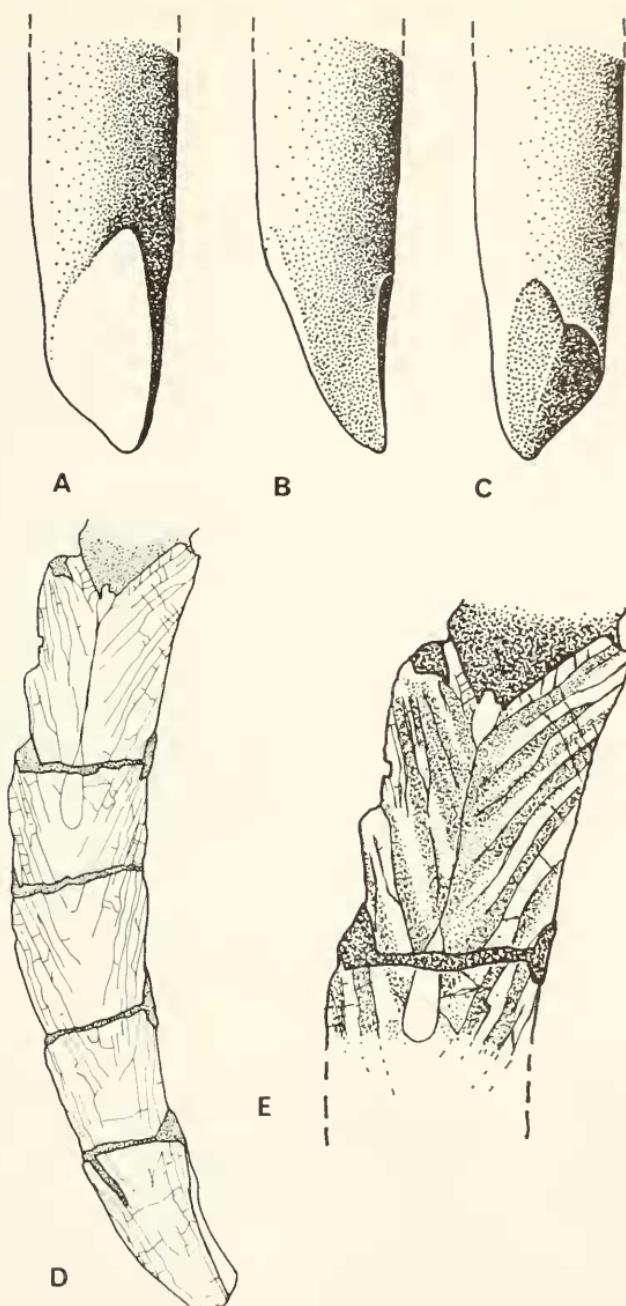


Figure 10. *Dinodontosaurus brevirostris*. A-C, right tusk of specimen MCZ No. 3452 showing wear facets, $x \frac{2}{3}$. A, lateral view; B, anterior view; C, medial view. D, E, longitudinal sections of part of tusk of specimen MCZ No. 3456. D, showing system of cracks, $x \frac{2}{3}$; E, showing pattern of bands in dentine, $x 1$.

DINODONTOSAURUS PLATYGNATHUS sp. nov.

Holotype. No. 65-XI-14-5 Museo de la Plata, La Plata, Argentina, fragmentary skull and lower jaw. Collected by the 1964-1965 expedition of the Museo de la Plata and the Museum of Comparative Zoology.

Horizon and locality. From an exposure in the Triassic Chañares Formation, about 1½ miles north-north-west of the point where the Gualo River emerges from the Plano del Gualo, in western La Rioja Province, Argentina.

Referred material. Specimen No. 149R, Divisão de Geologia e Mineralogia, Ministerio das Minas e Energia, Rio de Janeiro.

Description. The type specimen consists only of the palatal and occipital regions of a large skull, and of an almost complete lower jaw (Fig. 11). The bluntly-ending snout and the presence of downwardly directed canine tusks show that the specimen probably belongs to the genus *Dinodontosaurus*. The anterior end of the lower jaw, however, is elongated and tapers to a relatively thin

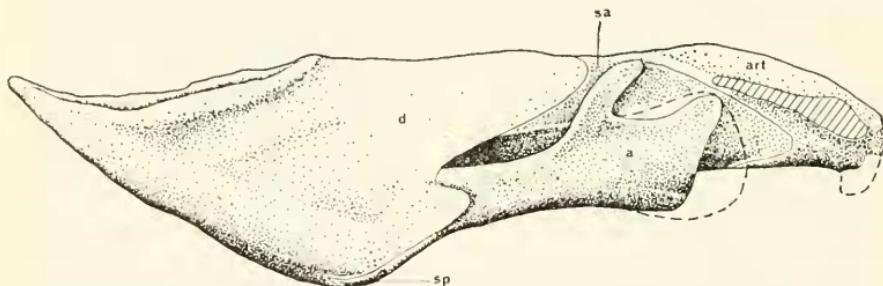


Figure 11. *Dinodontosaurus platygnathus*, type specimen. Lateral view of lower jaw, $\times \frac{1}{3}$ (for abbreviations, see p. 26).

point, unlike that of *Dinodontosaurus turpior*. It at first seemed likely that this was merely an aberrant type of distortion, but the existence of an almost identical lower jaw (specimen No. DGM 149R) in the Rio de Janeiro collection from the Santa Maria Formation of Brazil makes this explanation less plausible, and suggests instead that a different species of *Dinodontosaurus* may be represented. The fragments of the palate and occiput associated with the type specimen unfortunately do not show any other features by which the species could be distinguished from *D. turpior*, but it is felt nevertheless that the characters of the lower jaw merit specific distinction as *Dinodontosaurus platygnathus*.

KANNEMEYERIID REMAINS FROM THE CHAÑARES FORMATION

Specimen MCZ No. 3459 comprises a large left scapulocoracoid and clavicle; it was found about two miles east of the Mogote del Gualo (see Romer and Jensen, 1966, fig. 2).

The scapulocoracoid is badly flattened. As preserved, it has a total length of 63.5 cm, the scapula itself being about 48 cm long (Fig. 12). The scapula is very markedly constricted, being only 8 cm across at its narrowest point but expanding to 25 cm wide at its upper end. Most of the spine down the outer surface of the scapula has been eroded away but, from the width of its base and from the contours of the surrounding bone, the spine was clearly well developed and its dorsal end rose rapidly upwards from the blade. A groove runs down the inner surface of the lower end of the scapula. This groove leads to the coracoid foramen, which lies within the precoracoid bone.

The incomplete clavicle measures 33.5 cm along its outer surface, which is slightly convex longitudinally.

As discussed in an earlier paper (Cox, 1965), the shape of the scapula seems to be one of the diagnostic features of the two main families of Triassic dicynodonts. Short, wide scapulae are found in the Stahleckeriidae, which includes the other Chañares dicynodonts (*Chanaria* and *Dinodontosaurus*). Tall, narrow-waisted scapulae are, on the other hand, characteristic of the Kannemeyeriidae, which includes the genera *Kannemeyeria*, *Parakaninemeyeria*, *Sinokannemeyeria*, *Barysoma* and *Ischigualastia*. The scapula of MCZ No. 3459 is very similar to that of *Barysoma*, which is known from some postcranial material and an occipital plate from the Santa Maria Formation of Brazil (Romer and Price, 1944; Cox, 1965). The scapula of MCZ No. 3459 and that of *Barysoma* resemble one another closely in shape and in the position and strength of the spine. The scapula of *Barysoma* is, however, considerably larger; though incomplete, it is 55.5 cm long.

The single scapulocoracoid and clavicle of MCZ No. 3459 do not, of course, provide sufficient evidence to claim that *Barysoma* was present in the Chañares Formation or, alternatively, to erect a new genus or species of dicynodont. The specimen is merely evidence that the kannemeyeriid dicynodonts existed in Argentina during the time that the Chañares Formation was deposited. This is not surprising, since kannemeyeriids are known in Argentina both from the earlier Puesto Viejo Formation (Bonaparte, 1966a) and from the later Ischigualasto Formation (Cox, 1965).

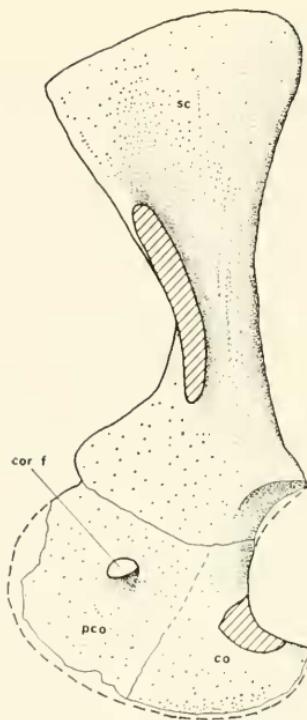


Figure 12. Scapulocoracoid of specimen MCZ No. 3459, $\times \frac{1}{8}$ (for abbreviations, see p. 26).

DICYNODONT REMAINS FROM THE TARJADOS FORMATION

A few fragmentary dicynodont remains were also collected in the transitional beds underlying the thick white sandstones which form the upper part of the Tarjados Formation. Specimen MCZ No. 3468 was collected just north of the Plano del Gualo, about one mile west of the Mogote del Gualo (see Romer and Jensen, 1966, fig. 2); it includes fragments of a skull and lower jaw. The maxilla encloses the proximal portion of a powerful tusk about 3.0 cm in diameter. This tusk shows traces of the alternating bands described above in *Dinodontosaurus brevirostris*, but also bears several longitudinal furrows. The remaining two specimens from the Tarjados Formation may also belong to the Dicynodontia: two fragments of large limb bones (MCZ No. 3469) and fragments of ribs (MCZ No. 3467).

THE AGE OF THE CHAÑARES FAUNA

The commonest Chañares dicynodont is *Dinodontosaurus brevirostris*. This species is extremely closely related to *Dinodontosaurus turpior*, which is the commonest dicynodont of the Santa Maria Formation of Brazil. The two species differ only in that the nostril of *D. brevirostris* is slightly closer to the front edge of the premaxilla, and its postorbital bone extends closer to, and further behind, the pineal foramen. This degree of similarity between their most abundant types of dicynodont is very strong evidence that the two faunas are very close in age. This is supported by the presence in both faunas of the peculiar elongated type of dicynodont jaw, which has here been named *Dinodontosaurus platognathus*. The Chañares fauna, however, lacks *Stahleckeria*, a dicynodont which occurs with *Dinodontosaurus* in the Santa Maria fauna; this suggests that the two faunas are not identical in age. In the slightly greater extent of its postorbital, *D. brevirostris* is more primitive than *D. turpior*, and it may well be ancestral to the Brazilian species; this suggests that the Chañares fauna is slightly earlier than the Santa Maria fauna.

Another fauna which appears to be earlier than that of the Santa Maria Formation is that of the Manda Formation of East Africa (Cox, 1965). This includes the dicynodont genus *Kannemeyeria*, found also in the early Triassic Cynognathus Zone fauna of South Africa, and differs from the Santa Maria fauna in containing a more primitive type of rhynchosaur (Colbert, 1958) and in lacking dinosaurs. Since both the Manda fauna and the Chañares fauna thus appear to be earlier than the Santa Maria fauna, it is necessary next to discuss the relative ages of these two faunas.

As just noted, the strong similarity between the dicynodonts of the Chañares fauna and those of the Santa Maria fauna strongly suggests that these two faunas are very close in age. In view of the considerable differences between the Santa Maria fauna and the Manda fauna, this further implies that the Chañares fauna is probably later than the Manda fauna. However, Romer (1966) has, on the contrary, suggested that the Chañares fauna is the earlier of the two. The evidence provided by the other elements of these faunas (cynodonts, pseudosuchians and rhynchosauroids) must therefore be examined.

The traversodontid *Massetognathus* is the only Chañares cynodont so far described (Romer, 1967). Each of the upper cheek teeth of this genus "shoulders" slightly into the one ahead; their crowns each bear two external cusps and a cross-ridge which lies

at the extreme posterior edge of the tooth so that the crown consists of a single basin. The traversodontid of the Manda fauna is *Scalenodon*, in which the upper cheek teeth do not "shoulder" into one another, the crown of the tooth bears only a single external cusp, and the cross-ridge lies more anteriorly, so that it divides the crown into anterior and posterior basins. The upper cheek teeth of later Triassic traversodontids such as *Proexaeretodon* and *Exaeretodon* of the Ischigualasto Formation, on the other hand, are similar to those of *Massetognathus*, but the "shouldering" of one tooth into the next is more pronounced. As Romer (1967: 20) states, "These differences suggest that *Scalenodon* is rather more primitive than the described South American forms." Furthermore, trirachodontid cynodonts are present in both the Manda Formation and in the earlier *Cynognathus* Zone fauna of South Africa, but are absent in the Chañares fauna. The relationships among all these cynodont faunas are thus more easily explained if the Chañares fauna is later than that of the Manda.

Romer (1966) has stated that the Chañares fauna contains small thecodonts similar to *Euparkeria* of the *Cynognathus* Zone. Other, more advanced pseudosuchians are also present, however, and our knowledge of the Chañares pseudosuchians is as yet too incomplete to provide any basis for a dating of the fauna.

Rhynchosaurs are absent from the Chañares fauna, but are found in both the Manda fauna and the Santa María fauna. As noted by Romer (1967), this fact is more easily explained if the Chañares fauna is older than that of the Manda and represents a time at which the rhynchosaurs were not yet developed as a major faunal element. However, rhynchosaurs are also unknown in two of the three localities in the Santa María Formation, and the composition of the fauna of these two localities is exactly the same as that of the Chañares fauna: dicynodonts (mainly *Dinodontosaurus*), cynodonts and pseudosuchians. Rhynchosaurs are known in the Santa María Formation only from a third locality, in which dicynodonts are absent (von Huene, 1935-42; Bortoluzzi and Barberena, 1967). These facts suggest that, though rhynchosaurs and dicynodonts are found together in the earlier Manda fauna, the ecological preferences of the South American type of rhynchosaur were distinct from those of the dicynodonts of these faunas, so that these groups are rarely preserved together — and it is relevant to note here the extremely specialised dental apparatus of the rhynchosaurs. If this is true, it is neither surprising nor significant that rhynchosaurs have not been found in the Chañares fauna.

To summarize, none of the evidence from the other vertebrate groups provides a convincing reason for rejecting the conclusion (based on the dicynodonts) that the Chañares fauna is only slightly earlier than that of the Santa Maria Formation of Brazil; it further appears to be later than that of the Manda Formation of East Africa.

One may next attempt to assess the relative ages of these South American Triassic faunas. The Chañares Formation of Argentina is somewhat older than the Los Rastros Formation, by which it is conformably overlain. On the other hand, it is also, on the evidence of the species of *Dinodontosaurus*, somewhat older than the Santa Maria Formation of Brazil, which may therefore be regarded as equivalent in age to the Los Rastros Formation of Argentina. Unfortunately, vertebrate fossils have not been found in the Los Rastros Formation, so it is impossible to confirm the equivalence by direct faunal comparison. The footprints of *Rigalites* from the Los Rastros Formation could, however, well have been made by one of the large pseudosuchians of the Santa Maria Formation (Bonaparte, 1966b).

There is also no unconformity between the Los Rastros Formation and the Ischigualasto Formation in the Chañares area, but merely a decrease in the amount of sandstone and an increase in the amount of clay and shale. Despite this lack of any break between the two formations, and the similarity between their cynodonts and rhynchosaurs, the archosaurs of the Ischigualasto fauna are considerably more advanced than those of Los Rastros/Santa Maria age.

Finally, it is impossible to equate these Gondwanaland vertebrate faunas to the standard German and Alpine divisions of the Northern Hemisphere Triassic with any degree of accuracy (Romer, 1966; Cox, 1967). One can at present only attempt to define the extreme limits between which these faunas must lie. As argued earlier, even the Chañares fauna is younger than the Manda fauna of East Africa. The latter contains the pseudosuchian reptile *Mandasuchus*, which is very similar to the genus *Ticinosuchus*, found in a definitely Anisian level of Monte San Giorgio, Switzerland (Krebs, 1965; Charig, MS in preparation). All these South American faunas are therefore probably post-Anisian. At the other extreme, even the Ischigualasto fauna is earlier than the Upper Norian, since it contains armoured pseudosuchians but lacks coelurosaurs and large dinosaurs (cf. Chowdhury, 1965). In fact, this fauna is probably somewhat earlier than Norian: Bonaparte (1966b), after reviewing the whole Ischigualasto fauna, has concluded that it is probably of Carnian age.

These conclusions are similar to those of Stipanicic, which are based upon evidence from fossil floras and ammonites, and which may be briefly considered here. The palaeobotanical evidence consists of the presence in the Los Rastros Formation (among others) of a flora which contains both Gondwanic *Dicroidium* elements and also a considerable number of Northern Hemisphere species (Stipanicic, 1957). Stipanicic points out (In press) that the northern species are known in the Northern Hemisphere only in deposits of post-Ladinian age. However, the range of these species into the earlier Triassic is still unknown, and this evidence therefore cannot yet be regarded as conclusive.

The ammonite evidence consists of the presence of specimens, identified by Barthel (1958) as *Cuccoceras* n.sp.aff. *cuccense* and *Beyrichites* sp., in beds lying under the igneous Pastos Grandes Group in Chile. According to Stipanicic (1967), this group practically interfingers with the Choioilitense Group of Argentina. Stipanicic (In press) believes that the Choioilitense Group is part of an igneous complex which is to be found below the various fossil vertebrate faunas and below the *Dicroidium* flora. Since the ammonites mentioned above indicate an Upper Anisian age, the overlying igneous complex and the fossil faunas and floras must all be post-Anisian. However, Kummel (personal communication) feels that the ammonite specimens are too incomplete for a definite taxonomic identification, and this line of argument must therefore be regarded as unproved.

SUMMARY

Three new stahleckeriid dicynodonts from the Chañares Formation of Argentina are described: *Chamaria platyceps* gen. et sp.nov., *Dinodontosaurus brevirostris* sp.nov., and *Dinodontosaurus platygynathus* sp. nov. A few post-cranial remains suggest that a kannemeyeriid dicynodont was also present.

Dinodontosaurus brevirostris is very closely related to *Dinodontosaurus turpior* of the Santa Maria Formation of Brazil, and is probably directly ancestral to it. The Santa Maria Formation therefore appears to be only slightly younger than the Chañares Formation, and equivalent to the Los Rastros Formation of Argentina.

The Chañares fauna is therefore younger than the Manda fauna of East Africa; this conclusion is supported by the cynodonts of these faunas. Though rhynchosaurs are absent from the Chañares fauna, this is also true of two of the three localities in the Santa Maria Formation, and their absence is almost certainly merely ecological.

The Chañares, Santa Maria and Ischigualasto faunas are, collectively, probably of Ladinian to Carnian age.

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LIST OF ABBREVIATIONS USED IN THE FIGURES

a	angular
art	articular
bo	basioccipital
bsp	basisphenoid-parasphenoid complex
co	coracoid
cor f	coracoid foramen
d	dentary
ect	ectopterygoid
eo	exoccipital
ept	epipterygoid
f	frontal
fmp	fenestra medio-palatinalis
ip	interparietal
j	jugal
l	lacrimal
mx	maxilla
n	nasal
op	opisthotic
p	parietal
pal	palatine
pc	processus cultriformis
pco	precoracoid
pmx	premaxilla
po	postorbital
pp	paraparietal
prf	prefrontal
pro	protoic
psp	parasphenoid

pt	pterygoid
q	quadrate
qj	quadratojugal
s	sphenethmoid
sa	surangular
sc	scapula
smx	septomaxilla
so	supraoccipital
sp	splenial
sq	squamosal
v	vomer